Mating behavior of the freshwater pulmonate snail, *Physa gyrina*

Thomas J. DeWitt

Department of Biology, State University of New York, Binghamton, New York 13902-6000, U.S.A.

Abstract. The typical mating sequence of freshwater pulmonate snails includes mounting, positioning, preputium eversion, intromission and dismounting. Previous studies report that sperm recipient behavior is passive or absent, and fecundity increases with size. I examined the mating sequence, mate rejection and fecundity of *Physa gyrina* (Say) removed from the Fenway in Boston, Massachusetts. Mate rejection occurred in any of four stereotypical ways: 1) shell swinging; 2) shell jerking; 3) increasing distance to the gonopore; 4) making head/preputium contact. The jerking behavior corresponds to what others described as sham copulation. Shell swinging was similar to parasite escape behavior. Fecundity increased with the size of sperm recipients but decreased with the size of sperm donors. Differences in methodology could explain discrepancies in the interpretation of mating behavior among studies.

Many studies have been conducted on the reproductive biology of freshwater pulmonate snails (Basommatophora; Geraerts and Joosse, 1984). Several behavioral studies, however, have reported conflicting observations within and among closely related taxa. This variation could be due to genetic variation and phenotypic plasticity, as well as differences in research methodology. The most complete information on basommatophoran reproductive behavior is for the sister families Lymnaeidae and Physidae. Physid snails have been studied recently in terms of predator induced life history shifts (Crowl, 1990; Crowl and Covich, 1990), macrophyte herbivory (Sheldon, 1987), sperm storage (Wethington and Dillon, 1991), parasite defense strategies (Townsend and McCarthy, 1980) and mate choice patterns (T. J. DeWitt, unpub. data).

Physa (=Physella) gyrina (Say) is widely distributed (Clarke, 1981) in lentic environments, especially where pollution or high temperatures exclude other snails (Clampitt, 1970; Harman, 1974). Physid snails, like lymnaeids, are hermaphrodites that usually cross fertilize but are capable of self fertilization (Colton, 1918; R. M. DeWitt and Sloan, 1959). Although the male genital tract can mature briefly before that of the female, it is unclear as to whether physids are ever functionally protandric (Duncan, 1959). Furthermore, snails can receive sperm regardless of the sexual maturity of female tracts, but can not oviposit (Duncan, 1959).

Peak breeding in the field for *Physa gyrina* is reported to occur from April through June in Iowa (Clampitt, 1970) and Michigan (R. M. DeWitt, 1955), although mature snails collected any time of the year will breed in the laboratory as long as water temperature exceeds 10°C (R. M. DeWitt, 1955). This corresponds to the April to May peak reported for *P. fontinalis* Linné by Duncan (1959) at a similar latitude.

In this paper, I report observances taken on the reproductive behavior of *Physa gyrina* removed from the field. I examined the typical mating sequence, mate rejection, and fecundity. Conflicting reports on mating behavior within and between pulmonate snail species could be due to research methodology.

METHODS

On six independent occasions between February and May 1990, 300-500 snails were collected from the same location in the Fenway in Boston, Massachusetts (NW of Beth Israel Hospital). Snails were collected between 1200 and 1600 hours. Dip nets were used to collect litter from the bottom of the Fenway (1-1.5 m depth). Snails were removed from the litter, by hand, to a bucket containing Fenway water. On all occasions, *Physa gyrina* made up over 98% of snail fauna [other species, in order of abundance, included *Planorbella campanulata (=Helisoma campanulatum)* (Say) and *Stagnicola elodes (=Lymnaea palustris)* (Say)]. Each collection, including all specimens, was brought back to the laboratory and placed in an aerated, filtered 38 *l* aquarium with approximately 20 *l* of water (half from the collection site, the other half was conditioned tap water). Population densities were greater than, but similar to those observed in the field during collection. Snails were kept at 20°C near a natural light source. They were fed canned or boiled vegetables (carrot, pea, chick pea). This diet was supplemented by unidentified algae in the aquaria.

Preliminary observations of snails were made to define criteria for successful versus failed copulation. Criteria I used to define successful mating were that 1) the sperm donor was in place at the shell margin of the recipient; 2) the preputium was placed in the immediate area of the gonopore; 3) the seminal vesicle within the preputium contained a milky

substance; 4) no agonistic behavior occurred within the first 30 seconds of mating.

TREATMENT 1

After approximately 18 hours from the time of collection, interacting *Physa gyrina* pairs were observed. As soon as the nature of each interaction was determined, pairs were removed and measured from the shell apex to the most distal portion of the shell margin. Sperm recipients from successful matings were removed to mason jars for a week and the number of eggs they laid was recorded. This continued until 12 successful matings were observed on each of the six occasions (72 observations total).

TREATMENT 2

An additional 90 *Physa gyrina* pairs were observed as in treatment one. In treatment two, however, pairs were not interrupted, but allowed to finish their interactions.

RESULTS

The sizes of sperm donors and recipients in treatment one were 7.32 ± 0.96 and 7.90 ± 1.12 (mean ± sd), respectively. The generalized mating sequence for *Physa gyrina* was similar to that described for *Lymnaea stagnalis* (Linne') (van Duivenboden and Maat, 1988), a closely related taxon, except that it occurred more rapidly. The sequence of successful mating included mounting (mate selection?), positioning, eversion of the preputium, intromission and dismounting. This process was sometimes interrupted by mate rejection but lasted approximately 10-20 minutes when successful (Fig. 1).

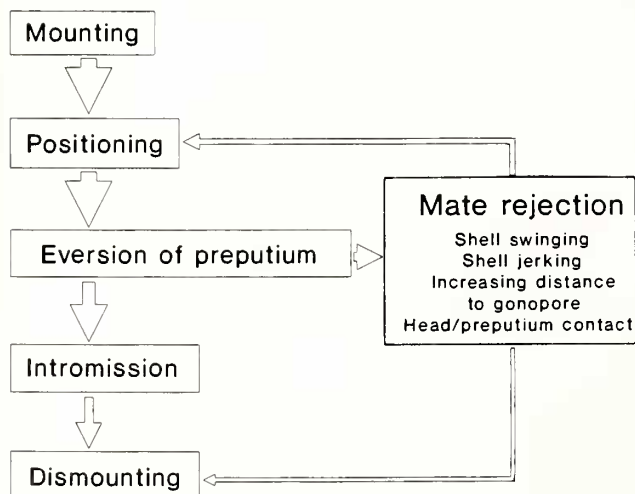Rejection of mates was observed to occur in four

Fig. 1. Mating sequence of *Physa gyrina*. Thickness of arrows approximates the frequency that path is followed.
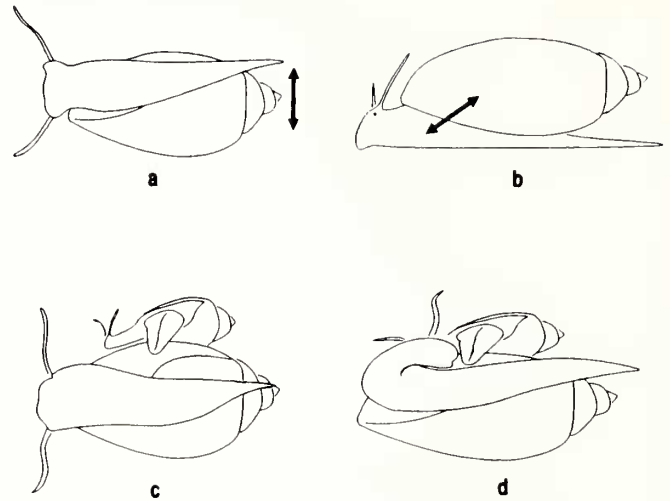

Fig. 2. Stereotypical mate rejection behavior by sperm recipients. a) shell swinging, b) shell jerking, c) increasing distance to gonopore, d) head/preputium contact.

stereotypical ways (Fig. 2). In order of decreasing frequency, intended sperm recipients performed 1) shell swinging, 2) shell jerking, 3) shell positioning such that sperm donors could not reach the gonopore, 4) head to preputium contact (''biting'').

Shell swinging was characterized by a 180-270° left and right twisting of the shell about the stationary foot. Shell jerking was rapid contraction of the shell toward the foot, with gradual release. This was generally repeated several times until the preputium was withdrawn. Shell positioning by intended sperm recipients occurred such that the distance from their shell margin to their gonopore was increased, effectively placing the gonopore out of reach of the sperm donor's preputium. I could not observe whether head to preputium contact included radular action but think it likely given that physid snails rarely cease radular movement and that the reaction from sperm donors was always immediate, violent withdrawal of the preputium, usually followed by immediate dismount. The first three forms of agonistic sperm recipient behavior generally resulted in two or three re-attempts at mating by sperm donors before they dismounted.

I commonly observed chain copulations of up to five snails, acting alternately as sperm donors and recipients. Furthermore, triads were observed on three occasions while collecting in the field. Polyandrous copulation, which has only been clearly described (among basommatophorans) for *Physa fontinalis* (Duncan, 1959), was not observed.

The range of snails observed to oviposit in this study was 6.3-10.9 mm. Larger sperm recipients proved significantly more fecund (R^2 for log transformed data = 0.58, $p_{\alpha/2}$ = 0.0001). However, the size of sperm donors was negatively correlated with sperm recipient (log transformed) fecundity (pearson correlated coefficient = -0.44, $p_{\alpha/2}$ < 0.01), even

when the size of sperm recipients was controlled for (partial correlation coefficient = -0.34, $p_{\alpha/2}$ = 0.025).

DISCUSSION

Describing the mating behavior of freshwater gastropods can be accomplished by field or laboratory studies. The former may be made difficult by turbid water, detritus, invasiveness of techniques used to locate snails and low probability of finding mating pairs. For these reasons, laboratory investigation is usually employed. This is acceptable if it is reasonable to believe organisms are behaving as they would in the field. Observations from field studies generally concur with laboratory findings (e.g. R. M. DeWitt, 1954b). However, it is likely that the laboratory techniques employed affect the behavior of animals being studied, and account for some of the variation in reported behavior.

R. M. DeWitt (1954a) reported 7 mm as the minimum size at which *Physa gyrina* would oviposit. However, this research of *P. gyrina*, and studies on other physids, suggest that the size at first oviposition varies among populations and species (Duncan, 1959; Clampitt, 1970; McMahon, 1975; Crowl, 1990). This variation could be due to physical variables such as temperature (McMahon, 1975) and plastic life history strategies. *P. virgata* (Gould) (Crowl, 1989; Crowl and Covich, 1989) is induced, by the presence of crayfish (predators), to delay reproduction until larger size is attained. I have observed similarly varied life history patterns in *P. heterostropha* Say in streams with and without goldfish in New York (unpub. data).

R. M. DeWitt (1954a) reported a lack of chain copulations in *Physa gyrina*. However, I observed chain copulation in the laboratory and field. Chain copulations have been reported for laboratory populations of several other freshwater pulmonates (e.g. Barraud, 1957; Duncan, 1959).

My observation of increasing fecundity as a function of snail size concurs with work on several freshwater pulmonates (e.g. R. M. DeWitt, 1954b; de Wit, 1955; Hunter, 1975; McMahon, 1975). However, this is the first report that the size of sperm donors is negatively correlated with the fecundity of sperm recipients. It will be interesting to see if studies employing different methods obtain similar results. The data from the present study do not allow me to address why larger sperm donors could have suppressed sperm recipient fecundity.

Many studies report that females are passive during mating (R. M. DeWitt, 1954a; Duncan, 1959). Van Duivenboden and ter Maat (1988) state "characteristic female mating behavior is absent". I observed several stereotypical female behavior patterns which I interpret to be mate rejection (Fig. 2). Two of these correspond to behavior reported by other investigators. Shell swinging is similar to weak parasite avoidance reported for *Physa fontinalis* in response to

chemicals from predatory leeches (Townsend and McCarthy, 1980). Shell jerking is similar to the description of "false coupling" given by Barraud (1957) and "sham copulation" given by van Duivenboden and ter Maat (1988) for *Lymnaea stagnalis*. Barraud (1957) describes false coupling as when the female gonopore remains unoccupied while the preputium is bent around her shell margin, despite contorted retractions of the female. Van Duivenboden and ter Maat describe sham copulation as "characterized by strong withdrawal of the forepart of the female, after which she relaxes again...while the preputium remains in place (under the female shell margin — not in the gonopore)." Barraud (1957) report that males may move away without copulation after this event and that copulation was seldom successful. Van Duivenboden and ter Maat (1988) report that nearly all copulations were eventually successful but "sham copulations occur frequently ($\geq$ 50% of the pairs)".

I believe the phrase "sham copulation" could be a misnomer because the interpretation as mate rejection is strongly supported in this study and that of Barraud (1957). Natural selection should provide strong selection pressure for successful copulatory mechanisms between conspecifics (Ridley, 1983) unless there is a benefit to unsuccessful mating behavior. Let us examine potential costs and benefits of sham (or unsuccessful) copulation. The only benefit I could associate with sham copulation would be the ethological argument that the practice is valuable for future "true" copulation. Noland and Carriker (1946) show that prior experience increases copulatory success in *Lymnaea stagnalis*. However, later studies by Barraud (1957) and van Duivenboden and ter Maat (1988) refute this. Costs of "sham copulation" could go beyond time and energy expenditure. Predation risk may be greater for animals in a pair versus solitary animals [e.g. *Gammarus pulex* (Linné); Ward, 1986]. Thus, the value of sham copulation is dubious. I suspect that the long period of isolation used in many studies made sperm donors less willing to give up copulation attempts, thereby reducing the occurrence of successful mate rejection and delaying or preventing straightforward copulation.

Researchers often use the isolate-unite technique (e.g. Noland and Carriker, 1946; Barraud, 1957; Duncan, 1959; van Duivenboden and ter Maat, 1988) to study the reproductive behavior of gastropods. This protocol is effective for stimulating copulation, but could lead to overlooking phenomena of more realistic situations for field populations (e.g. mate choice). The protocol could introduce artifact problems as well [e.g. sperm deprivation during isolation eventually leads to initiation of self fertilization (van Duivenboden, 1983), thereby reducing receptivity to mating].

It is probable that a more generalized view of mating behavior in gastropods can be obtained by supplementing the isolate-unite technique with studies using multiple wild-caught snails in as close conditions to their natural environment as

possible (i.e. population density, water, temperature, light, etc.). The use of focal pair sampling (perhaps videotaping) would also be more likely to yield valuable details on mating over multiple pair observation (e.g. van Duivenboden and ter Maat, 1988). The suggested techniques allow elucidation of structured mating, mate rejection and other phenomena occurring in wild populations.

ACKNOWLEDGMENTS

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